A MATHEMATICAL MODEL OF 'OHI'A DIEBACK AS A NATURAL PHENOMENON

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INTRODUCTION

By means of a very general model system, the possibility of interdependent dying, as contrasted to individual, random dying, in large areas of forest is investigated. In particular, insight is provided into the possible roles of natural mechanisms in producing such interdependent collapse behavior and what the properties of such mechanisms must be. In this study, mechanisms of change in the forest are characterized as "natural" if they have been part of the forest environment over an evolutionary time scale. Otherwise, they are characterized as "introduced."

This model is applied to the problem of dieback in the native 'ohi'a (Metrosideros collina subsp. polymorpha) forests of Hawai'i. The focus of the model is on the "trigger" of the dieback. That is, we look only at the transition of trees from a healthy to a declining state (or vice versa). Mechanisms at work in the subsequent death or reinvigoration of trees are beyond the scope of this model.

The model allows separate examination of the effects of interaction between trees, external factors affecting growth, and physiological factors. Thus, it gives insight into the relative importance of various features of the 'ohi'a dieback phenomenon.

It is of especial interest for 'ohi'a dieback to know whether natural factors could produce interdependent decline or whether an "introduced" epidemic (e.g., disease or insects or some combination of introduced factors) is necessary to explain the field observations. The model presented here, while very general, deals with the plausibility of these various types of mechanisms for interdependent dieback.

Before discussing the model considered in this paper and its application to 'ohi'a dieback, the value of such models from physics in biological problems and the kind of information they

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can be expected to provide will be considered (Weidlich 1971; Callen & Shapero 1974).

Problems of the sort considered here concern the behavior of "incompletely-specified systems." That is, they deal with systems (e.g., a forest) for which there is either insufficient data to predict the behavior of each individual or incomplete knowledge of the laws which govern individual and system behavior, or both. In fact, these systems are intrinsically incompletely specified since we are not really interested in predicting the detailed behavior of each individual and since the data necessary for that task is impossibly extensive. Incompletely specified systems are probabilistic systems by their nature. The subdiscipline of statistical mechanics in physics is directed at such problems in Hamiltonian systems (Hobson 1971), and both models and methods originally developed in physics may be applicable to problems of incompletely-specified systems arising in other contexts.

In particular, while the causes of interdependent behavior among atomic spins in magnets and interdependent behavior among 'ohi'a trees in a dying forest are obviously rather different, the statistical behavior of these two systems does show interesting similarities.

The most serious objection to the approach taken in this paper is that models from physics, like the one discussed below, are such an oversimplification of reality that their results cannot be relied upon. While this is always a danger, such difficulties can be minimized by focusing attention on features which are insensitive to specific details of the model. It is argued that the collapse behavior in the present study is such a feature. In addition, if detailed simulation is desired, it is often possible to add specifics to such models and successively improve the simulation of reality.

DESCRIPTION OF THE MODEL

Imagine a forest of N uniform-age, essentially identical trees. Let each tree be in one of two states: healthy or declining. (The effect of modifying this model to include individual differences in trees and continuous variation in vigor will be discussed below.) This simple, very general model shows the important features of transition from healthy to declining in a manner which is qualitatively the same as a more realistic model.

The forest of identical trees in two possible states can be modelled as a spin-½ classical magnet in two dimensions--the Ising model in statistical mechanics (Weidlich 1971; Callen & Shapero 1974). We use this analogy to analyze the behavior of our model forest. There are three important classes of variables in this problem:

(1) Tree interaction parameters which represent the effects of the trees on each other. We label these parameters I_{ij}, for the interaction between trees i and j. Since we consider only a single species in this model, the I_{ij} represent only intraspecific competition. Interspecific competition is treated as an individual (negative) growth factor in its effects on the trees. These parameters are analogous to spin-spin interactions in magnets.

(2) Individual growth factors which influence the tree toward the healthy or declining state. These factors represent the net effect on each tree of such influences as limiting resources, disease or insect attacks, moisture relations, and interspecific competition. They may be favorable or unfavorable. We label these factors G_i for tree i, $i=1,\ldots,N$. These factors are analogous to local magnetic fields in the magnetic systems.

(3) A stand condition parameter which represents the relative susceptibility of trees to stresses which might induce dieback. We label this parameter S. Large S characterizes stands which are resilient in meeting stress and resist the transition from healthy to declining. The magnitude of S will depend on tree physiology, including maturity and other factors which affect resistance to stress. Such factors may include environmental restrictions to a tree's ability to respond to stress; for example, substrate limitation of root development. This parameter plays a roll in the model analogous to inverse temperature in the magnetic system.

We study the simplest case: i.e., we assume that the individual growth factors are the same for all N trees in the stand; and we assume that there is no tree interaction except for pairs of trees which overlap in canopy, rhizosphere, etc. (i.e., close neighbors). Hence, $G_i = G$, independent of which tree is considered, and $I_{ij} = I$ if trees i and j overlap, while $I_{ij} = 0$ otherwise.

So the picture is of N trees interacting with close neighbors and under the influence of a growth factor, which may either induce or retard growth. Some of these trees are healthy, and some are declining. The susceptibility of trees to transition from healthy to declining is governed by a stand condition parameter.

MODIFICATIONS AND RELEVANCE TO 'OHI'A DIEBACK

The two basic assumptions of the model are that the trees are identical and that there are two discrete states for the trees: healthy or declining. It is, however, possible to relax these assumptions. Since 'ohi'a is a pioneer species on new lava flows in Hawai'i, often with a readily available seed source from an adjacent, older lava flow, and since it does not regenerate in its own shade, it tends to grow in uniform-age stands (Mueller-

Dombois 1977). Of course the trees are still not identical: there are genetic and micro-environmental differences which produce differences in trees. However, since these variations are limited by the nearly uniform seed source, age, and macro-environment of a stand, they can be accounted for by allowing our parameters, I_{ij}, G_i, and S, to vary from tree to tree (i.e., to vary with i and j) with a limited distribution.

The assumption of two discrete states for the trees can be replaced by a continuous spectrum of tree vigor or by the possibility of a tree's state being described as a mixture of the healthy and declining states. The latter suggestion actually seems most reasonable since trees do die in stages and sections --e.g., the crown may die but leave vigorous trunk sprouts (Mueller-Dombois 1977).

It is clear that the model, even with relaxed assumptions, oversimplifies the description of a stand of 'ohi'a trees in nature. For this reaaon, we only address questions of general behavior which are not likely to depend critically on the details of the model. In particular, the presence or absence of widespread decline (i.e., of interdependent collapse behavior like a phase transition) is insensitive to the modifications described above, with the possible exception of allowing the stand condition parameter, S, to vary from tree to tree. (Allowing S to vary removes the concept of an equilibrium "temperature" and suggests that the forest is not in internal equilibrium.) However, S should only vary over a narrow range through a given even-aged stand and hence can be treated as approximately constant in the systems of interest to this study. The effect of variations of S with a restricted distribution will be to broaden the "phase transition" so that it does not occur so sharply in time and space. But interdependent collapse behavior will still be evident in such a system.

In sum, then, the modifications needed to make the proposed model more realistic will not affect the qualitative nature of any interdependent collapse which occurs. Hence, one can with some confidence draw conclusions from this model relative to the plausibility of various possible trigger mechanisms for 'ohi'a dieback.

BEHAVIOR OF THE MODEL

In the steady state, we can express the behavior of the model described above in terms of the steady-state probability, $P(h)$, that the forest stand consists of h percent healthy trees. In detailed analysis of the model, we find that $P(h)$ depends on the three parameters, I, G, S, only in the two combinations G times S and I times S. So we introduce two new parameters: $g = GS$, and $k = IS$. That the state of the forest depends on the parameters of the model in these combinations accords well with our expectations for biological systems: the effect of a given

environmental stress (negative G) depends not only on the magnitude of the stress but also on the resilience of the forest (i.e., on stand condition, S). And similarly for the effects of competition.

Figure 1 shows a sequence of $P(h)$ for $N = 100$ with relatively large k and three values of g. These curves illustrate the possibility of interdependent change of a stand from healthy to declining condition.* Such a situation could occur if the effect of the trees on each other (through nutrient depletion for example) were quite strong, while the conditions for growth measured by G fluctuated from favorable to unfavorable in an extreme year.

When the individual growth factors or the stand condition parameter are neutral, so $g = 0$ (Fig. 1[b]), the forest stand is in a critical state. The probability that the stand will be predominantly declining is the same as that it will be predominantly healthy. So small fluctuations could cause a collapse from healthy to declining. The converse is also possible: the use of fertilizers, thinning, or similar techniques to make growth more favorable could revive a stand which has begun to die back. An alternative outcome might be the growth of separate healthy and declining regions within the larger stand. For the case where $g = 0$, one could have about equally large clumps of dying trees and of healthy trees. The establishment of such clumps will be a function of microenvironment. This may be what happens in a "hot spot"--the small patches of dieback in dryland areas.

For contrast, Figure 2 shows a similar sequence of $P(h)$ but with $k = 0$. There is no bimodality here because there is no interdependent response. Rather, examination of the model shows that the change from a healthy to a declining stand takes place randomly by individual trees in this case, resulting in random thinning. To get as strong a dieback condition (or as strong a healthy condition) as in Figures 1(a) and (c) requires much larger values of g ($g = 1.0$ when $k = 0$ gives about the same condition as $g = 0.02$ when $k = 2.5$). So the swings in growth factors have to be much greater to produce a recognizable dieback when interaction between trees does not play a significant role. An introduced disease could produce such a large change in g. However, relatively light environmental stress may be sufficient to produce collapse when it is associated with interactions between the trees. Such light stress could easily be produced by changes in nutritional status, moisture, or other environmental constraints.

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* The mathematical expression of the model and its analysis to produce the curves discussed here are being prepared for separate publication. The analysis and results are very similar to Weidlich (1971).

We see from the two figures that interactions between trees introduce an interesting kind of stability, with an associated fragility, into the forest system. The stability comes from the tendency of the forest to maintain its state even for relatively small g. However, once g becomes negative, there is a tendency for the whole system to "collapse." Hence a fragility, when close to critical values of the growth factors and stand condition parameter, is closely connected with the stability of the forest.

DISCUSSION AND CONCLUSIONS

The motivation for this work has been to examine the plausibility of the hypothesis that natural mechanisms within the 'ohi'a forest ecosystem can produce an interdependent collapse of a forest stand.

As illustrated in the previous section, the simplified model discussed here does show such behavior. It has been noted that the modifications required to make the model realistic do not change the qualitative behavior of the collapse, which is the focus of our interest. We see that collapse due to a natural mechanism is a possible outcome which is an alternative to random thinning, or, in a more extreme case, to introduced epidemic. The reason that collapse occurs rather than random thinning is related to the way in which 'ohi'a stands are established as pioneer, uniform-age stands on new lava flows with no regeneration in their own shade.

The fact that dieback in 'ohi'a forests seems to occur only in fairly mature forests, perhaps at intervals of several hundred years, suggests that the magnitude of environmental stress (i.e., the reduction in g) required to produce collapse is quite large and hence unusual. This fact also suggests that the interaction parameter, which increases as the trees get larger and more able to affect one another, must be fairly large. In addition, S will be larger for mature trees than, for example, for seedlings. So the requirements for collapse (i.e., that k be large and g go from a significant positive value to a significant negative value) are associated with the long time scale of several hundred years from establishment of the stand to dieback. This long time scale has made the collapse more difficult to recognize as a natural phenomenon in the sense addressed here. Similar phenomena on a shorter time scale have been much easier to recognize.* For example, one could apply the same type of model to the yearly dieback of annual plants. Annual life-forms provide a mechanism to respond to environmental stress (sharp decrease in G). This

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* The example given here was originally suggested to me by N. Balakrishnan.

decrease in G (perhaps accompanied in some cases by a decrease in S) leads to a very rapid transition of a stand from healthy to declining. The response pattern which has been illustrated in Figure 2 would serve for this example as well.

This study also suggests that it would be profitable to seek out ways of measuring the interaction parameter, I, in the field to verify the interaction mechanism suggested here for 'ohi'a dieback. This parameter will include all factors which cause of environment. For example, nutrient competition will bring about similar deficiencies in neighboring trees when nutrients are depleted below a critical level. Since this effect is due to interaction between trees, it is one of the components of the parameter I. All such components must be considered.

SUMMARY

The possibility of collapse of the 'ohi'a forest from healthy to dying condition due to natural factors is investigated by means of a very general mathematical model. The model is closely related to the Ising model of magnetism. The role of interactions between the trees, i.e., intraspecific competition, is contrasted with the roles of environmental stress, disease, or insect epidemic in producing a collapse of the model forest. It is argued that the collapse behavior persists through modifications of the model which bring it into closer correspondence with reality. Study of the model leads to the following conclusions: (1) Canopy collapse can plausibly be triggered by natural mechanisms including competition, as well as by introduced epidemic factors. (2) Collapse is an alternative to random thinning or external epidemic, any of which can occur in the model under appropriate conditions. (3) Investigation of interaction mechanisms between trees in the 'ohi'a forest is an especially important and potentially rewarding avenue for further research.

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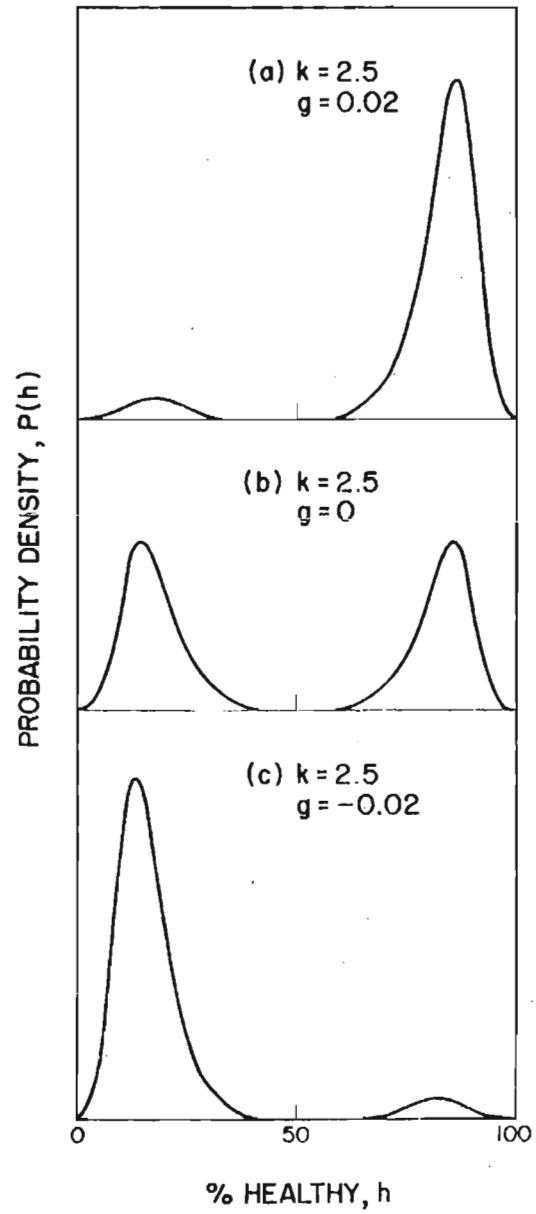

FIGURE 1. Probability distribution for healthiness of forest stands with strong interactions between trees.

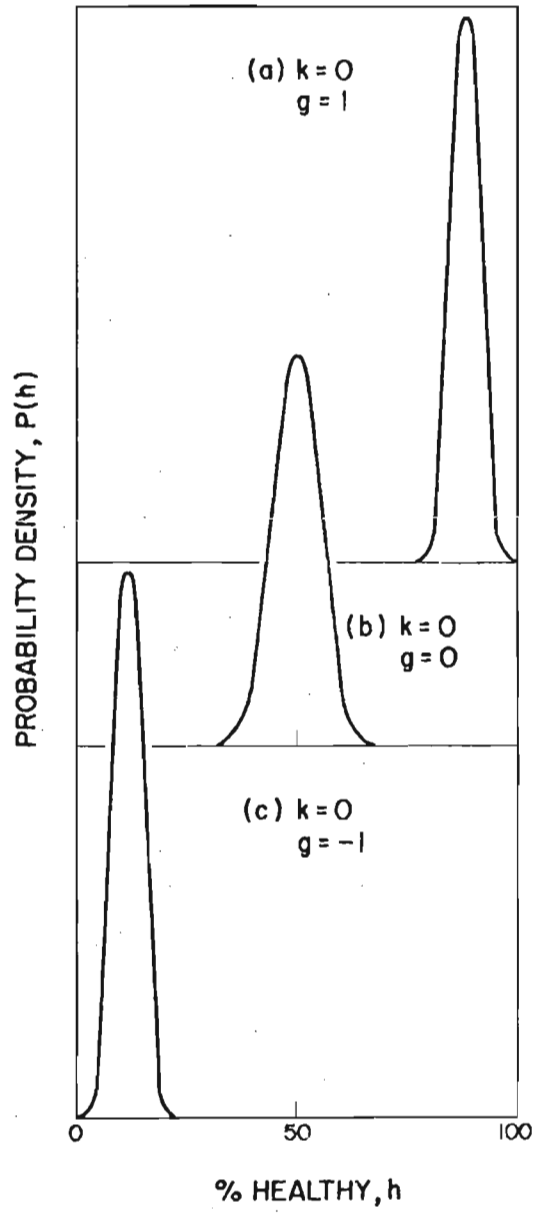

FIGURE 2. Probability distribution for healthiness of forest stands with no interactions between trees.